

# The First Historical Extinction of a Marine Invertebrate in an Ocean Basin: The Demise of the Eelgrass Limpet *Lottia alveus*

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**Abstract.** *Lottia alveus*, a gastropod limpet once found only on the blades of the eelgrass *Zostera marina* from Labrador to New York in the western Atlantic Ocean, is the first marine invertebrate known to have become extinct in an ocean basin in historical time. The last known specimens were collected in 1929, immediately prior to the catastrophic decline of *Zostera* in the early 1930s in the North Atlantic Ocean. The brackish water refugium of *Zostera* throughout the decline was apparently outside of this gastropod's physiological range, and the limpet became extinct. Few marine invertebrates have habits as specialized and ranges and tolerances as narrow as did *L. alveus*. The fact that most marine invertebrates have large effective population sizes may account for their relative invulnerability to extinction.

## Introduction

There are no reports of the post-Pleistocene extinction of any marine invertebrate, in spite of the fact that hundreds of terrestrial and freshwater species of animals and plants have become extinct as human activity has increased around the world (Martin and Klein, 1984; Vermeij, 1986; McNeely *et al.*, 1990). This is perhaps even more remarkable given the widespread perception that many marine invertebrate species have suffered extensive decimation and that a number of them are on endangered species lists (for example, Gee and Wilson, 1981; Franz, 1982; Wells *et al.*, 1983; Wicksten, 1984).

We report here the first historical extinction of a marine invertebrate from an ocean basin. The limpet *Lottia alveus* (Fig. 1), a once abundant stenotopic species that ranged from southern Labrador to Long Island Sound and lived only on the blades of the eelgrass *Zostera marina* (Conrad, 1831; Couthouy, 1839; Gould and Binney, 1870), is now extinct in the Atlantic Ocean. Here we consider the evidence for this conclusion and suggest why this extinction occurred.

## Materials and Methods

### Field studies

Eelgrass populations were searched specifically for limpets in the following locations: Cape Cod, Massachusetts, between 1979 and 1982; along the eastern Connecticut shore (Fishers Island and Long Island Sounds) between 1982–1987 and 1989–1990, and at Vinalhaven (25 km east of Rockland), central Maine in 1984 (J.T.C. and D.A.C.); at Boothbay Harbor (45 km southwest of Rockland), central Maine in 1971, and in Newfoundland (Come by Chance, in Placentia Bay, and at Norris Point, Bonne Bay, in the Gulf of St. Lawrence) in 1990 (G.J.V.). We contacted biologists who are familiar with the common Atlantic limpet *Tectura testudinalis* (= *Acmaea testudinalis*) and who have sampled *Zostera* epiphytes in Quebec (Rimouski), Nova Scotia (Halifax), Maine, Massachusetts, Rhode Island, and Connecticut. Since 1965, *L. alveus* has been searched for without success in south-central Nova Scotia, and in Labrador and Newfoundland (D. Davis and R. Noseworthy, pers. comm., respectively). We examined



**Figure 1.** Dorsal and lateral views of the extinct Atlantic limpet *Lottia alveus* (a pre-1900 specimen from Massachusetts, ANSP 39044, 1.6 $\times$ ). The laterally compressed shell of this limpet precisely fitted the narrow blade of the eelgrass *Zostera marina*.

all published records (from 1831 to 1989) of shallow-water marine mollusks and eelgrass biota from the Arctic Ocean to the central Atlantic coast of the United States.

#### Museum studies

We examined 14 museum malacological collections in search of specimens of *L. alveus*. For systematic purposes and for trophic analyses, we studied radulae of alcohol preserved and rehydrated specimens of *L. alveus*, as well as radulae of *L. alveus parallela* and illustrations of the radula of *L. alveus angusta*.

These collections are located in the following museums (abbreviations are given for museums cited later in the text): Academy of Natural Sciences, Philadelphia (ANSP); American Museum of Natural History, New York; British Columbia Provincial Museum, Victoria (BCPM); California Academy of Sciences, San Francisco; Los Angeles County Museum of Natural History; Museum of Comparative Zoology, Harvard University (MCZ); Museum of Paleontology, University of California, Berkeley; National Museums of Canada, Ottawa; New York State Museum, Albany (NYSM); Natural History Museum, London [formerly British Museum (Natural History)]; Nova Scotia Museum, Halifax; Santa Barbara Museum of Natural History, Santa Barbara, California; United States Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); University of Alaska Museum, Fairbanks (UAM).

In addition, a number of major United States herbarium collections of the eelgrass *Zostera marina* from North America were examined in an independent study on eelgrass wasting diseases by F. Short, who has provided us with his records of dried limpets found on herbarium sheets.

## Results

### *Systematics and biogeography*

The limpet *Lottia alveus* (Conrad) was described in 1831 from Massachusetts. It is more commonly known as *Acmaea alveus* or *Collisella alveus*. We follow the nomenclatural revision of Lindberg (1986) in referring this species to *Lottia*. Two situations led to the previously overlooked history of this limpet in the North Atlantic Ocean. First, there was a persistent belief that *L. alveus* was an ecotype of the rocky intertidal limpet *Tectura testudinalis* (Müller, 1776) (Dall, 1871; Johnson, 1928; Abbott, 1974), and that it was thus not a separate species. Second, there are continued reports of its presumed presence on the Atlantic coast in molluscan checklists and books (for example, Abbott, 1954, 1974; Emerson and Jacobson, 1976).

However, as Jackson (1907) and Morse (1910, 1921) clearly demonstrated, *L. alveus* is distinct from *T. testudinalis* in anatomy, behavior, shell shape, sculpture, and color. Morse (1910) noted that shells of the two species could be distinguished at "a millimeter or more" in length, by sculpture, apex shape, and color. McLean (1966) further noted that *L. alveus* was not a form of *T. testudinalis* that had settled on eelgrass blades, as both *T. testudinalis* and the eelgrass *Zostera marina* are common in European waters, where *L. alveus* does not occur. William Healey Dall, whose opinion was widely regarded by contemporary malacologists, also concluded, in a reversal of his earlier belief (Dall, 1871), that *L. alveus* was "a good species" (Sumner *et al.*, 1913). He was apparently influenced by the findings of Jackson (and perhaps Morse), but his opinion apparently did not reach the general malacological community.

McLean (1966) and Lindberg (1986) have shown that *L. alveus* and *T. testudinalis* are properly placed in different genera. The genus *Lottia* possesses a single pair of reduced marginal teeth (uncini) that are present at the posterior end of the ribbon segment. The genus *Tectura* lacks these marginal teeth on the radula. Lindberg (1981, 1986, 1988) discusses the phylogenetic importance of these radular characters in diagnosing limpet genera. Jackson (1907) detailed other differences between the radulae of the two species, although he failed to illustrate the uncini.

*Lottia alveus* originated in the North Pacific Ocean from an ancestral lineage represented in the Mio-Pliocene of Japan by *Lottia angustitesta* (Yokoyama, 1926) (Yokoyama, 1926; Kotaka and Ogasawara, 1974; D.R.L., in prep.). The Western North Pacific Ocean is also considered the center of origin in the Tertiary of *Zostera* (McRoy, 1968; den Hartog, 1970). Both *L. alveus* and *Zostera* invaded the North Atlantic Ocean through the Bering Strait and the Arctic Ocean in the late Tertiary,

as did numerous other marine organisms (Durham and MacNeil, 1967; G.J.V., in prep.).

Pleistocene glaciation subsequently created three allopatric subspecies: *Lottia alveus parallela* (Dall, 1914) in the Northeast Pacific, *Lottia alveus angusta* (Moskalev, 1967) in the Northwest Pacific, and *Lottia alveus alveus* (hereafter, *L. alveus*) in the Northwest Atlantic. The three subspecies are distinguished on the basis of external morphology and radulae (D.R.L., in prep.). In addition, the Atlantic subspecies had markedly less variation in color and shell pattern than Pacific populations, and also possessed a widespread radular abnormality (an extra first lateral tooth on the left side of the radula) absent in Pacific individuals. These characteristics in the Atlantic subspecies suggest a founder effect. Mitochondrial DNA analysis (of the extant North Pacific populations and of preserved material of the North Atlantic populations) may aid in resolving whether these three taxa should be treated as full species.

*Lottia alveus parallela* occurs only on *Zostera* between Kazuna Bay, Cook Inlet (60° North Latitude) in southern Alaska (UAM, N. Foster collections, 1975) and Smith's Inlet in Queen Charlotte Sound, British Columbia (51° North Latitude) (BCPM, late nineteenth century specimens). Dall (1921) cites a southern Pacific coast limit of *L. a. parallela* as Victoria, British Columbia (48° North Latitude), but the specimen lot in BCPM upon which this record is apparently based indicates that the material may also have been collected at Skidegate Inlet, on the east coast of Queen Charlotte Island. Burch (1946) cites what appears to be an independent Victoria record, but without data, and we have been unable to locate supporting material. We know of no formal searches in Alaska or British Columbia that have attempted to establish the exact distribution of *L. a. parallela*. *Lottia a. angusta* has been recorded only from Sakhalin Island, Sea of Japan (46° North Latitude), on *Zostera* (Moskalev, 1967).

*Lottia alveus* was known as far west (south) on the Atlantic coast as Long Island Sound, where it was recorded from New York by De Kay (1843) and Letson (1905) (see also Table I, herein) and from Stratford, Connecticut by Linsley (1845). It occurred as far east (north) as Egg Harbor, Labrador (USNM, O. Bryant collections, 1908) (Fig. 2).

#### *The last known populations*

No eelgrass limpets have been collected in the Atlantic Ocean since 1929 (Table I). The previous known range of this limpet (Labrador to New York) has been searched thoroughly by us and others. Given the planktotrophic larva that lottiid limpets possess (Lindberg, 1981), and the now widespread occurrence and availability of *Zostera* as a habitat, we do not believe that there are refugial,

isolated "pockets" of this limpet in remote coves, offshore islands, or similar sites.

Two live collected USNM specimens (13.0 and 9.3 mm in length) of *L. alveus* bear a label indicating the place of collection as Cape Ann, Massachusetts (50 km northeast of Boston) and a date of 14 July 1953. We have excluded this record from Table I for the following reasons. In contrast to the records listed in Table I, we have been unable to verify that this is the date of collection (for example, by other species collected at the same time and place by the same collector, by knowledge of the collector's specific activities at the time and place of collection, and so forth). The collector (J. A. Weber) specialized (as a hobby) in collecting gastropod radulae, and obtained material from many sources. Thus he may, for example, have obtained preserved or dried material of this limpet from another shell collector (Weber made a long trip up the coast in 1953, visiting shell collectors and collecting specimens). The specimens were received at the Smithsonian Institution in 1966; while the Latin name and location are part of the original writing, the date has been added in black ink at a later time. Dexter (1968) systematically sampled the mollusks at five widely separated stations at Cape Ann from 1933 to 1937 and from 1956 to 1961, and in many intervening years through 1967. While finding many uncommon and rare species, he never found *L. alveus* (R. Dexter, pers. comm., 1990). Dexter specifically examined the mollusks on eelgrass blades at Cape Ann in 1949 (Dexter, 1950), again without finding *L. alveus*. Dexter was also at Cape Ann in July 1953, where he did not find *L. alveus* in informal surveys of the eelgrass, nor did he meet Weber there (R. Dexter, pers. comm., 1990).

We do not discount this record because it occurs after 1929, nor because it does not fit our view of the timing of the extinction of this mollusk. The possible persistence of *L. alveus* until the early 1950s does not alter our conclusion that this limpet is extinct. Many extinctions are characterized by a lengthy and slow decline of a species, rather than by the precipitous disappearance documented here. Thus, one scenario for the demise of *L. alveus* would have been a catastrophic bottleneck followed by the eventual disappearance of the last remnant populations over subsequent decades. Rather, we reject this record because decades of sampling and collecting mollusks specifically at Cape Ann, and in the Boston area in general, before and after 1953 have failed to discover this limpet. It is not infrequent to find on museum labels transmittal dates, exchange dates, and cataloging dates, and we thus suggest, pending other confirmation, that "1953" is one of these dates-of-record.

The last verifiable report of living eelgrass limpets in the Atlantic Ocean is that of Proctor (1933). Collecting in 1929 (*vide* Johnson, 1929) at Bar Harbor on Mt. Desert





Figure 2. Former populations (dots) of the limpet *Lottia alveus* in the Northwest Atlantic Ocean. Triangles represent other localities mentioned in text.

Island on the northeastern Maine coast. Proctor reported that "One may go to the Narrows [near Bar Harbor] at low tide today and find . . . thousands of individuals readily accessible . . ." Proctor believed (evidently on the basis of shell color and shape) that *L. alveus* and *T. testudinalis* were identical species. Their abundance may have been a source of his confusion. It is possible that he found dislodged *L. alveus* individuals upon rocks and errant *T. testudinalis* individuals on eelgrass blades. There are reports of *L. alveus* from rocks (Stimpson, 1851; Jackson, 1907; Morse, 1910) that Morse (1910) believed to be the result of specimens detached by waves and storms. *Lottia alveus* was on occasion also found on other substrates. There is, for example, a specimen (MCZ) collected in 1897 at Isle au Haut, Maine, attached to the periwinkle *Littorina littorea* (Linnaeus, 1758), bearing the label, "living thus on this specimen of *L. littorea* which was on

(a) float . . . in bed of eelgrass." The typically rock-dwelling limpet *Lottia pelta* (Rathke, 1833) can be found occasionally in California on the blades of the surfgrass *Phyllospadix* when dense stands of the latter overlap intertidal rocks (J.T.C., pers. observ.)

#### *Reconstruction of the biology of Lottia alveus*

The morphology, anatomy, habitat, and collection records of *Lottia alveus* permit a partial reconstruction of the biology and natural history of this extinct Atlantic species. There are no studies of the extant subspecies in the North Pacific Ocean.

#### *Abundance*

As with many now uncommon animals and plants reported as "common" or "abundant" in the nineteenth

century, there are no quantitative analyses of the population size or structure of *Lottia alveus*. However, a sense of the abundance of this eelgrass limpet can be gleaned from the literature (Table II). It is clear that this limpet was sufficiently common throughout much of northern New England that it could be collected "on demand" between the 1860s and the late 1920s. While workers continued to refer to *L. alveus* in later years [for example, Miner's (1950) statement, "found abundantly on eelgrass"], it is clear that these are references to older literature and collections.

### Trophic ecology

The radula of *L. alveus* was illustrated by Jackson (1907). We find it to be an accurate figure, with the exception of the missing uncini. Analysis of the radular morphology of *L. alveus* indicates that it was a trophic specialist, feeding upon the epithelial cells of the eelgrass, rather than upon epiphytic diatoms and algae. The radula of all *alveus* subspecies has broad, straight cutting edges on its first and second lateral teeth. It is analogous to the radula of the Northeast Pacific Ocean stenotopic surfgrass (*Phyllospadix*) limpet *Tectura paleacea* (Gould, 1853), which eats only the epithelial cells of that grass (Fishlyn and Phillips, 1980). With the exceptions of specimens that presumably wandered off or were dislodged from eelgrass, all reliable literature reports and museum material indicate that *Lottia alveus* was restricted to, and by our analysis ate only, the eelgrass *Zostera marina*. We predict that the extant subspecies in the North Pacific feed upon the epithelial cells of *Zostera*.

### Distributional ecology

We have studied all reported localities (including consideration of their probable nineteenth century shoreline

Table I

Final records of the limpet *Lottia alveus* in the Atlantic Ocean

Locality	Last known collection	Reference
New York: Long Island:		
Noyack Bay	1926	(1)
Massachusetts: Boston region	1921	(2)
Maine: Rockland	1922	(3)
Maine: Mt. Desert Island	1929	(4)
New Brunswick: Bay of Fundy: Grand Manan	1920	(5)
Quebec: Saguenay County: Sept-Iles	1925	(6)

References: (1) NYSM, R. C. Latham, collector; (2) Thompson, 1921; (3) Lermond, 1922; (4) Johnson, 1929; (5) ANSP, H. S. Colton, collector; (6) ANSP, on *Zostera* herbarium sheet.

Table II

Records of the abundance of the limpet *Lottia alveus* on the Atlantic coast of North America

Locality and date	Remarks	Reference
"New England", 1860s	"Found abundantly on the eel-grass"	Gould and Binney, 1870
Grand Manan Island, Bay of Fundy, 1890	"very abundant on eel-grass at low water"	Ganong, 1890
Isle au Haut, Maine, 1893-1897	[>1000 specimens in many lots]	MCZ
North Haven, Maine [25 km east of Rockland], 1908	"very common on <i>Zostera marina</i> "	Jackson, 1908
"Maine", 1909	"very common all along the coast, on eel grass and occasionally on rocks"	Lermond, 1909
Boston region, 1910	"in certain places hundreds may be collected in a short time"	Morse, 1910
Rockland, Maine, 1922	75 specimens taken on eel grass in one afternoon, incidental to other collections	Lermond, 1922
Mt. Desert Island, Maine, 1929	"thousands of individuals readily accessible" at low tide	Proctor, 1933

configurations) for *Lottia alveus* from Long Island Sound to Labrador to reconstruct aspects of the distributional ecology of this limpet.

Although no authors reported the salinity of the water in which they collected, it appears that all localities in which *L. alveus* was collected were and are characteristic of fully marine (32-33‰ or greater), rather than estuarine, habitats. Of course it is difficult to establish the salinity of a locality without actual records, but no collections indicate that populations of *L. alveus* were maintained on eelgrass in low salinity (brackish water) sites. Further evidence may be sought in the associated biota: the mollusks reported to have been collected with or in the immediate vicinity of *L. alveus* (for example, Rathbun, 1881; Jackson, 1908; Winkley, 1909; Thompson, 1921; Lermond, 1922) include strictly marine species, as well as euryhaline species, but never was the co-occurring molluscan fauna (nor authors' site descriptions) characteristic of strictly brackish water.

We conclude that *L. alveus* was probably a stenohaline species of open coastal waters. We predict that extant sub-

species of *L. alveus* in the North Pacific will be found to be stenohaline.

## Discussion

### *An extinction scenario*

What factors led to the extinction of this limpet? We suggest a scenario that focuses upon a combination of the stenotopic habitat of this species and its apparently narrow physiological range.

Between 1930 and 1933, *Zostera* precipitously disappeared from both the eastern and western North Atlantic Ocean on a scale and in geographic breadth far exceeding any previous historical declines (Rasmussen, 1973, 1977). The dramatic decline of this eelgrass led to extensive disruptions in neritic ecosystems, including large reductions in migratory waterfowl populations, loss of commercial scallop fisheries, and alterations for decades of nearshore soft sediment habitats (Rasmussen, 1977; Short *et al.*, 1987). Until now, however, no extinctions have been attributed to this decline. The primary cause of this decline was probably a "wasting disease" caused by the slime mold *Labyrinthula* (Muehlstein *et al.*, 1988; Short *et al.*, 1986, 1987, 1988). More than 90% of the standing stock of *Zostera* was eliminated with concomitant and often striking changes in associated biota (Stauffer, 1937; Dreyer and Castle, 1941).

Populations of *Zostera marina* survived, however, in low-salinity refugia (Short *et al.*, 1986). As argued above, we suggest that *Lottia alveus* was probably a stenohaline species; collection records indicate that it did not, unlike *Zostera*, extend into brackish waters. We speculate that the presumably narrow salinity range of this limpet may have prevented it from surviving on refugial eelgrass populations in lower salinity waters.

In contrast, the sacoglossan opisthobranch *Elysia ca-tulus* Gould, 1870, similarly restricted to and feeding solely upon eelgrass (Clark, 1975), did not become extinct. This small sea slug ranges from Boston, Massachusetts (Johnson, 1915) to Virginia (Clark, 1975), and probably south to the southern limit of *Zostera* in the Carolinas (Jensen and Clark, 1983). Eelgrass populations were similarly eliminated throughout *Elysia's* range, except, as noted, in brackish water. We suggest that *Elysia* did not become extinct because it lives in salinities at least as low as 17‰ (Marcus, 1972), and thus survived the eelgrass blight in the estuarine eelgrass refugia.

It remains possible, of course, that factors other than the putative osmoregulatory abilities (which cannot now be experimentally determined for Atlantic populations) prevented *L. alveus* from extending into brackish waters. These factors could include respiratory intolerance of the clay-silt loads typical of estuarine environments, or the build-up of sediments or epiphytes in brackish water on

eelgrass blades that may have inhibited the limpet's feeding. For whatever reasons, the evidence suggests that *L. alveus* did not occur in the upper bay environments in which *Zostera* survived.

Further evidence for this scenario is gained by the observation that other eelgrass-associated gastropods also found refugia in other habitats or on *Zostera* in lower salinity waters. Snails typically found on eelgrass in New England and the middle Atlantic coast include the pro-sobranchs *Lacuna vineta* (Montagu, 1803), *Bittium alternatum* (Say, 1822), *Bittium varium* (Pfeiffer, 1840), *Crepidula convexa* Say, 1822, and *Mitrella hnata* (Say, 1826) (Nagle, 1968; Marsh, 1973). None of these is restricted to *Zostera*, and none became extinct, although there are reports of changes in microhabitat and abundance following the eelgrass decline (Dexter, 1962; O'Connor, 1972). Russell-Hunter and Tashiro (1985) have similarly noted the decline of the *Zostera*-associated in-faunal bivalve *Cumingia tellinoides* following the disappearance of eelgrass beds.

The survival of *Lottia alveus parallela* and *Lottia alveus angusta* may result from the fact that no extensive areas of eelgrass were eliminated in the North Pacific Ocean (den Hartog, 1987).

### *Other reported marine mollusk extinctions*

Other marine mollusks have been reported as possibly extinct. We have found no records of any other documented historical marine invertebrate extinctions.

A single living specimen of the limpet "*Collisella*" *ed-mitchelli* was collected in the early 1860s in southern California (Lindberg, 1984). Nothing is known further of the Holocene history or habitat of this otherwise Pleistocene species. The Caribbean bivalve *Pholadomya candida* was believed extinct (Runnegar, 1979), but it is extant in waters off Venezuela (Gibson-Smith and Gibson-Smith, 1981). The nudibranch sea slug *Doridella batava*, once believed to be endemic to the Netherlands, is reported as possibly extinct (Wells *et al.*, 1983), but has been found living in France (Platts, 1985). Moreover, *D. batava* may represent an introduction of a previously described species from elsewhere in the world (Wells *et al.*, 1983; T. Gosliner, pers. comm., 1990).

Six to eight species of brackish water hydrobiid snails were reported as possibly extinct on the United States Atlantic coast by Morrison (1970). The distinction of these undescribed species from still living and closely related taxa has not been demonstrated (F. Thompson, pers. comm., 1986), nor is it clear that searches were made for still extant populations.

The most intriguing record that we have found is that of the Californian potamidid estuarine snail *Cerithidea fuscata*, which Taylor (1981) reported as "possibly ex-



tinct." This high intertidal, mudflat-dwelling horn snail is known only from San Diego Bay in southern California; it was last collected in 1935. Taylor (1981) suggested that threats to its existence were "pollution, dredging, and land fill." Taylor (1981) treated *C. fuscata* Gould, 1857, as a distinct species, with *Cerithidea sacrata hyporhyssa* Berry, 1906, in synonymy. Grant and Gale (1931) and Bequaert (1942) considered the latter a synonym of *Cerithidea californica* (Haldeman, 1840). The status of *C. fuscata* as a species distinct from *Cerithidea californica*, rather than either an ecophenotype or subspecies, has not been clarified (J. McLean, pers. comm., 1986). *Cerithidea fuscata* differs from other populations of *Cerithidea* by virtue of its smooth, tapered shell with flat whorls (Berry, 1906). While *C. californica* is common and widespread both to the north and south, the smooth-shell population has long been considered to occur only in San Diego Bay (Burch, 1945). There are no details of population declines or disappearances of *C. fuscata* as yet documented, nor is there published evidence that searches have been made for extant populations. Nevertheless, that populations of *Cerithidea*, whose life history is characterized by non-planktonic larvae (Race, 1981), are susceptible to bay-wide extinctions has been documented elsewhere (Carlton, 1976).

It is clear from these and other reports that there are historical records of marine and estuarine mollusks with small and geographically limited populations, and that some of these populations are believed to have disappeared. There are also many species of crustaceans, annelids, flatworms, hydroids, and other invertebrates that have never been reported since the nineteenth century. Some of these are from coastal localities that have been obliterated during the course of human population expansion and concomitant littoral urbanization. Finally, at both local (state) and international levels, various marine invertebrates have been reported as "endangered." Listings for marine mollusks have been achieved in part due to the collecting activities of shell collectors. We distinguish all of these records from demonstrably extinct taxa.

### Conclusions

With its specialized feeding habits and narrow habitat range, *Lottia alveus* conforms well to the profile of species that are believed to be highly susceptible to extinction (Martin and Klein, 1984; Vermeij, 1986). The limited geographic range (a consequence of Pleistocene glaciations), the limited trophic range (an adaptation dating from the Mio-Pliocene), and the presumably limited physiological range (a phylogenetic constraint shared by almost all lottiid limpets and perhaps dating from the Paleozoic origin of the group) were interwoven and cascading attributes that set the stage to make this species

vulnerable to extinction. We suggest that the refugia of *Lottia's* sole food source during a period of catastrophic decline were outside of this limpet's habitat range, and the limpet became extinct.

Most marine invertebrates whose biology and distribution are well-known do not have habits as specialized and ranges as narrow as did *Lottia alveus*. (There are, of course, a great many species described from only one locality, but whose actual ranges are not known). Most of those taxa that are known from one or a few host species have much wider geographical ranges than did this limpet. The fact that most marine invertebrates have large effective population sizes, often over broad ranges, may account further for their relative invulnerability to extinction in historical time. In contrast, small and geographically restricted populations of species (short-range endemics, for example) may be particularly vulnerable to extinction. Those species whose life history combines non-planktonic larvae with juvenile or adult stages not likely to be associated with drifting algae or wood may be specifically susceptible to extinction.

While our records to date indicate that marine invertebrates in general have escaped historical extinctions by the end of the twentieth century, human activities have been and are clearly capable of severely reducing and completely eliminating populations of marine invertebrates from extensive parts of their ranges. These actions have and will continue to fundamentally alter the structure of natural communities.

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